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# A spinose appendage fragment of a problematic arthropod from the Early Ordovician of Morocco

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A highly spinose fragment of a possibly raptorial appendage from the Arenig (Early Ordovician) of the Upper Fezouata Formation north of Zagora, southeastern Morocco is described as the arthropod *Pseudoangustidontus duplospineus* gen. et sp. nov. The single fragmentary specimen displays a unique morphology, carrying at least 39 pairs of spines (i.e., 78 spines) of very regularly alternating lengths. *Pseudoangustidontus* gen. nov. shows some similarities to a number of spinose arthropod appendages and appendage parts, most notably to the spine-bearing podomeres of the third prosomal appendage of megalograptid eurypterids and the problematic and incompletely known genus *Angustidontus*. However, megalograptids and *Angustidontus* both have a lower spine count, while the latter also carries only a single row of spines. Because no known arthropod displays a morphology closely comparable to that of *Pseudoangustidontus* gen. nov., the affinities of the new fossil within Arthropoda remain uncertain.

Key words: Arthropoda, raptorial appendage, Arenig, Ordovician, Morocco.

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## Introduction

Spinose raptorial appendages are known from a wide range of arthropods (Fig. 1). The spines on the appendages are generally used to impale prey, as for example in the terrestrial amblypygid, thelyphonid and schizomid arachnids, the marine spearing stomatopod crustaceans and the terrestrial mantid insects. Apart from directly wounding prey, spines can also function to subdue and immobilize it by simply entangling it, as observed in amblypygids (Ladle and Velander 2003; Weygoldt 2000). The purpose of this paper is to describe an enigmatic, extremely spinose raptorial arthropod appendage fragment from the Arenig (Early Ordovician) of the Upper Fezouata Formation north of Zagora, southeastern Morocco (Fig. 2).

## Geology

Traditionally, the classical British nomenclature for the Ordovician (Fortey et al. 1995, 2000) has also been applied to Morocco. The first two stages of this regional British system, the Tremadoc and the Arenig, can be correlated to the international global stages as follows: (1) the British Tremadoc corresponds to the global Tremadocian stage; (2) the British Arenig encompasses the entire global unnamed second stage of the Ordovician, and the base of the global unnamed third stage (Gradstein et al. 2005; Ogg 2004; Webby et al. 2004). For the global unnamed second stage, the name "Floian" was recently proposed (Bergström et al. 2006) and this name will be used further in the text. For the purpose of this discussion, stage names will be given as: British Stage/ Global stage. The Upper Fezouata Formation is a geographically extensive, mainly transgressive unit composed of yellow-green mudstones and siltstones, becoming increasingly sandy towards the top. In the area around Zagora, southeastern Morocco (Fig. 2A), where this unit reaches its maximum thickness of up to 700 m, it conformably overlies the siltstones of the Lower Fezouata Formation of Tremadoc/ Tremadocian age (Early Ordovician) and locally grades into the sandstones of the middle Arenig/ late Floian (Early Ordovician) Zini Formation (Destombes et al. 1985). The age of the Upper Fezouata Formation is constrained between the early to middle Arenig/early to late Floian (Early Ordovician).

Because the present specimen was found by local Moroccan collectors and reached the authors via a rather circuitous route, it has been impossible to identify the exact locality where it was found with absolute certainty. At least six sites to the north of Zagora are known to preserve labile parts (Fig. 2B). In addition to these sites, local Moroccan collectors have also started working at a number of other outcrops in the area. One of the largest and most intensely worked excavations is situated approximately 25 km north

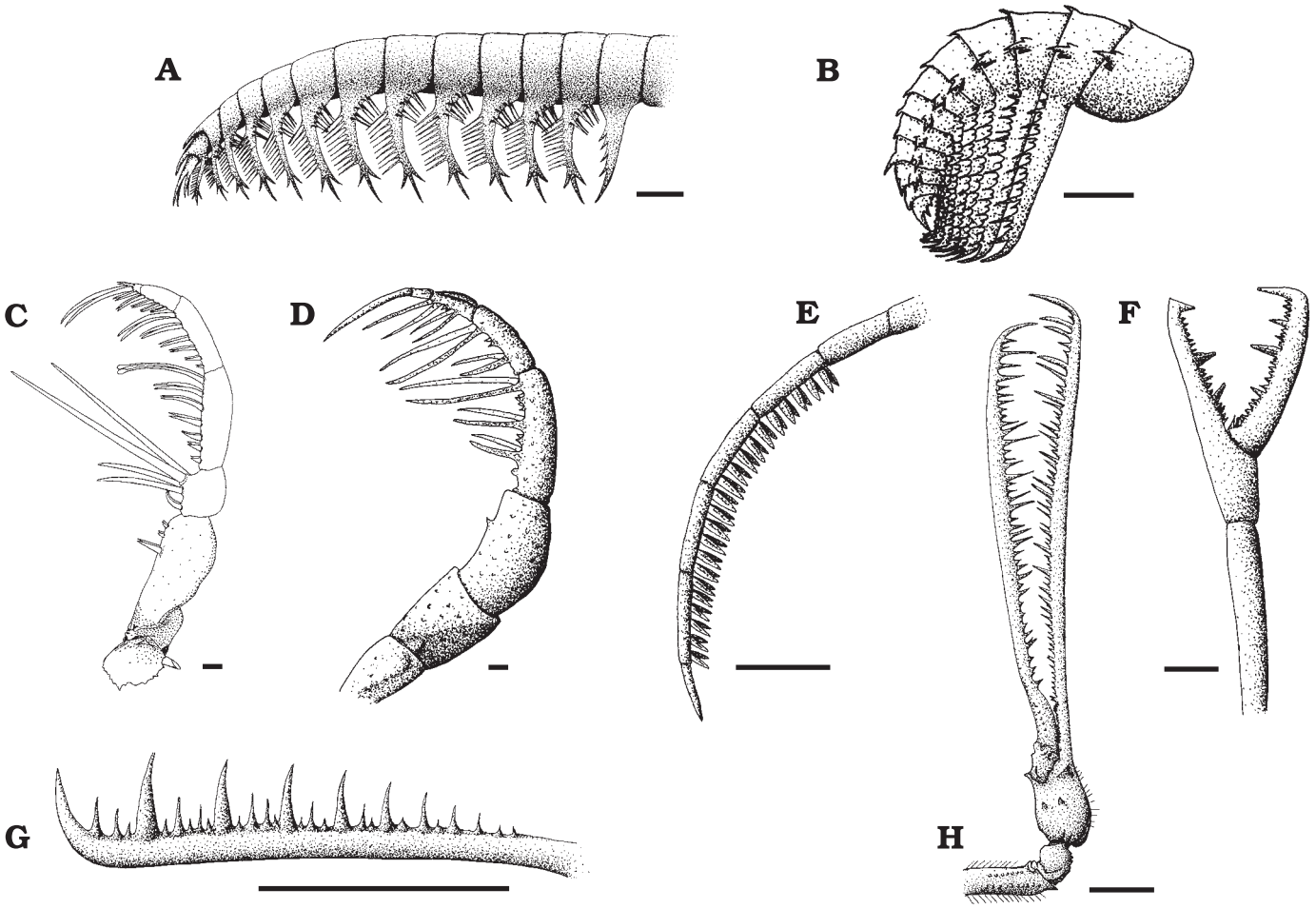



Fig.1. Several types of spinose arthropod appendages discussed in the text. **A**. Spiculate first appendage of the anomalocaridid *Anomalocaris briggsi*, Early Cambrian, Australia (redrawn from Nedin 1995). **B**. Pectinate first appendage of the anomalocaridid *Laggania cambria*, Middle Cambrian, Canada (redrawn from Dzik and Lendzion 1988). **C**. Third prosomal appendage of the megalograptid eurypterid *Megalograptus ohioensis*, Late Ordovician, USA (reproduced from Caster and Kjellesvig-Waering 1964). **D**. Third prosomal appendage of the mixopterid eurypterid *Mixopterus kiaeri*, Early Devonian, Norway (redrawn from Størmer 1934). **E**. Third prosomal appendage of the laurieipterid eurypterid *Ctenopterus cestrotus*, Late Silurian, USA (redrawn from Clarke and Ruedemann 1912). **F**. Chelicera of the pterygotid eurypterid *Erettopterus osiliensis*, Late Silurian, Estonia and USA (observations of O.E.T.). **G**. *Angustidontus weihmannae*, Late Devonian, Canada (drawing based on photograph in Copeland and Bolton 1960). **H**. Cheliped of the decapod malacostracan *Thaumastocheles zaleucus*, Recent, Caribbean region (redrawn from Tshudy and Sorhannus 2000). Scale bars 10 mm.

of Zagora (locality number 6 in Fig. 2B). It is located near the top of the Upper Fezouata Formation, and hence is of middle Arenig/late Floian age. Since the lithology of the matrix in which the specimen is preserved is similar to that of the above-mentioned excavation, it seems plausible that the specimen was found at this site.

## Materials and methods

Preparation of the specimen was carried out with the aid of a Wild M5 stereomicroscope and fine needles. The specimen was drawn wet, with main lighting consistently coming from the upper left. Drawings were prepared at a magnification of × 12 using a Wild M5 stereomicroscope with attached Wild T10 drawing tube. The fossil was photographed dry, with unpolarised light coming from the upper left. Photographs were taken using a Canon EOS 300D digital SLR camera with a Sigma EX 50 mm F 2.8 DG Macro lens with the aperture value stopped down to f45 for maximal depth of field. The light sensitivity of the camera was set to 100 ISO.

## Systematic palaeontology

### Phylum Arthropoda von Siebold, 1848
### Class, Order and Family uncertain
### Genus *Pseudoangustidontus* nov.

*Type and only species*: *Pseudoangustidontus duplospineus* sp. nov.

*Derivation of the name*: Composition of *pseudo-* from Greek *pseudes*, meaning "false", and the generic name *Angustidontus* (Latin, "narrow

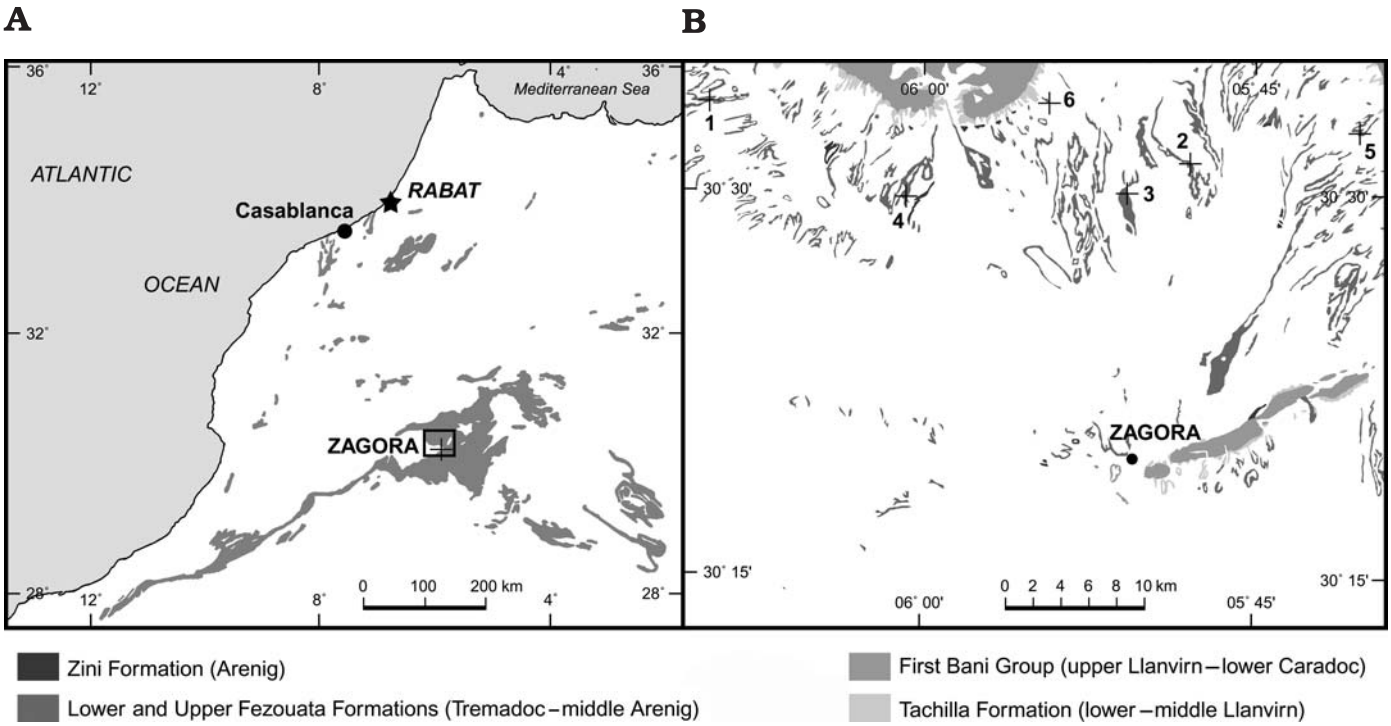



Fig. 2. **A**. Geographical situation of Ordovician surface outcrops in Morocco, indicated in medium grey (adapted from Destombes et al. 1985). The rectangular marquee indicates the area shown in detail in **B**. Geographical situation of Ordovician surface outcrops to the north of Zagora according to the geological map (sheet 273, Zagora—Coude du Draa). Localities indicated with cross-hairs are numbered in stratigraphical order, with 1 and 2 being situated close to the boundary between the Lower and Upper Fezouata Formations.

toothed"), previously (Cooper 1936) given to another problematic arthropod genus known only from disarticulated parts. The name is intended to indicate that there are certain similarities of the present fossil to *Angustidontus* Cooper, 1936, while at the same time it also emphasizes that important differences separate these genera.

*Diagnosis*.—As for species.

## *Pseudoangustidontus duplospineus* sp. nov.

Figs. 3, 4.

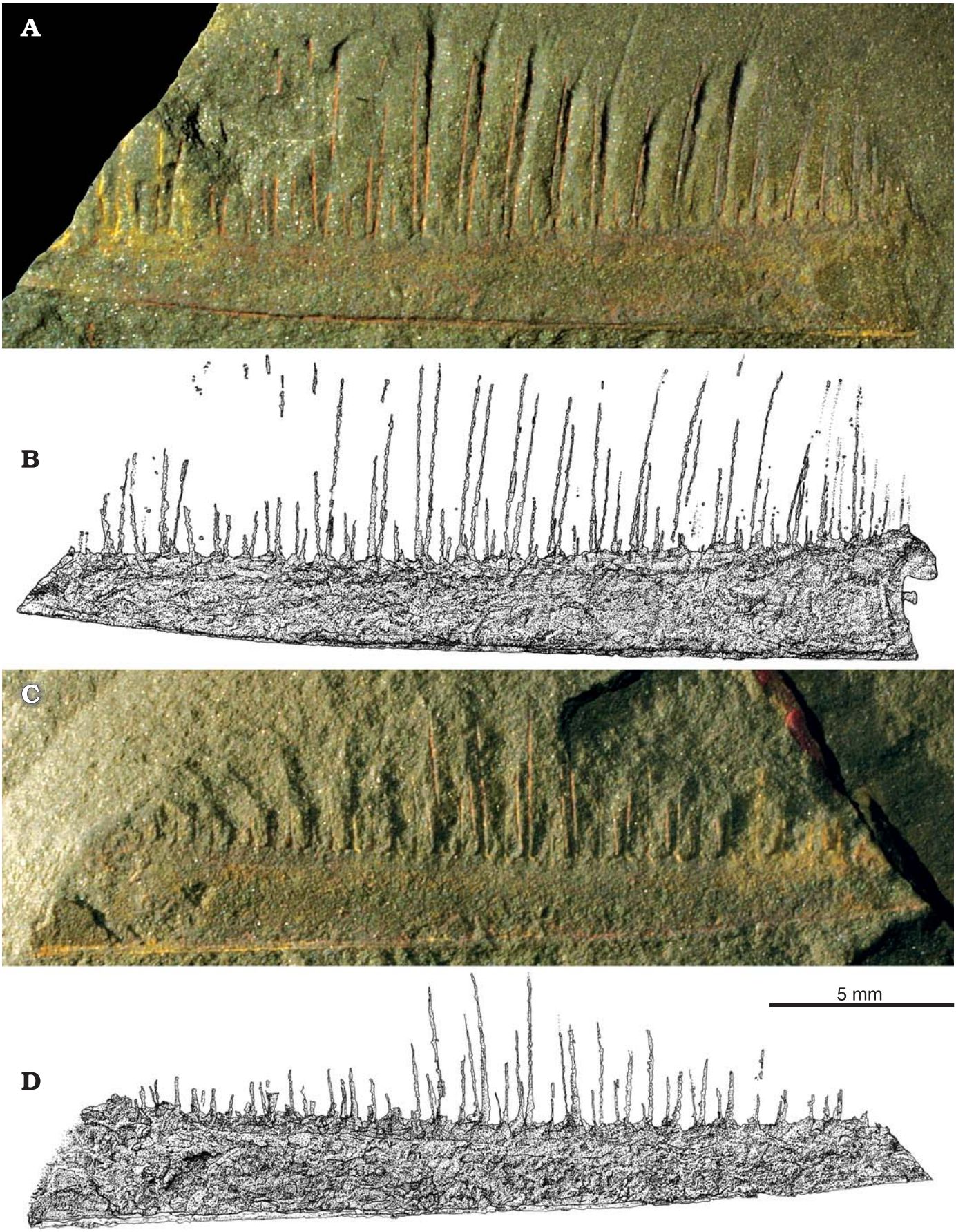
*Holotype*: Holotype and only known specimen housed in the collections of The National Museums of Scotland, Edinburgh under accession number NMS G.2005.119.1 (part and counterpart).

*Horizon and occurrence*: The middle Arenig/late Floian (Early Ordovician) of the Upper Fezouata Formation to the north of Zagora, Anti-Atlas, southeastern Morocco [exact locality uncertain].

*Etymology*: Composition of *duplo-* from Latin *duplus*, *-a*, *-um*, meaning "double", and *spineus* from Latin meaning "thorny, spiny". The specific name is intended to reflect the presence of double rows of spines.

*Diagnosis*.—Unmineralised, slightly curved, elongate, tapering appendage fragment, ca. 25 mm long. Convex-curving side with narrow carina and concave-curving side carrying at least 39 pairs of evenly spaced spines (i.e., at least 78 spines) set in a V. Spine pairs show very regular alternation of spine lengths, with long spine pairs alternating with short spine pairs approximately 1/3 the length of the long spine pairs.

*Description.*—The fragmentary specimen consists of both a part (Fig. 3A, B) and counterpart (Fig. 3C, D). Maximal preserved length is 24.8 mm, and maximal height excluding spines is 3.5 mm. Although clearly sclerotised, the specimen does not show any evidence for mineralisation of the cuticle. The fossil tapers towards one end and is slightly curved. Along the convex curved side runs a narrow, well-defined carina (height 0.17 mm) which becomes less distinct towards the tapering end of the specimen. On the opposite side, the concave curvature is strongest in the widest third of the specimen. This side carries an impressive array of long, slender, regularly spaced spines. Two rows of overlying spines are preserved on clearly different levels, becoming increasingly separated from each other by the intervening matrix distally. In total, the specimen shows evidence of at least 39, and probably even 40 pairs of spines (i.e., 78–80 single spines) set in a narrow V. The first seven or eight pairs of spines situated on the widest side of the fossil appear to be placed slightly closer together than the remaining spines. Whereas along the first half of the fossil all spine pairs are almost superimposed on top of each other, they become gradually more separated distally. All spines were hollow. They widen towards their base and seem to have a gently oval cross-section, being slightly flattened laterally. At least two, and possibly three types of spines can be differentiated on the basis of their length. The first type has a preserved length of ca. 5.2 mm. Pairs of these spines alternate with the second type of shorter, slightly finer spines which attain a length of ca. 1.8 mm. The lengths of both types of alternating spines vary only slightly among themselves along the length of the speci-


A
B
C
5 mm
D

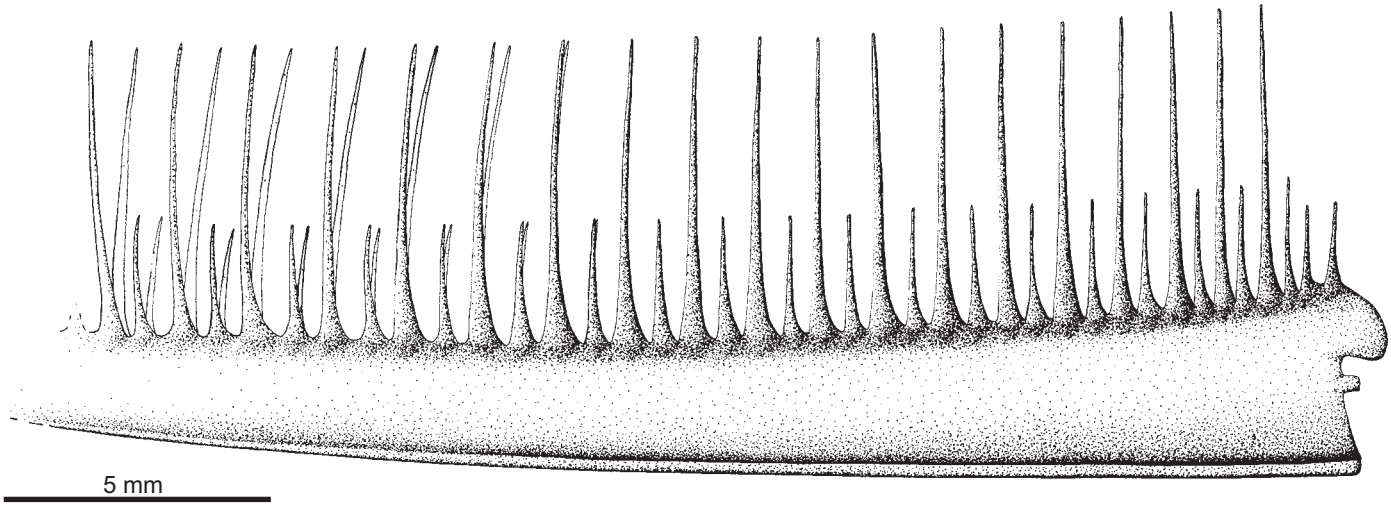



Fig. 4. Reconstruction of *Pseudoangustidontus duplospineus* gen. et sp. nov.

men. However, the poorly preserved first two spine pairs closest to the wide termination of the specimen may belong to a third type, appearing finer and slightly shorter than the second spine type with an estimated length of only ca. 1.4 mm.

*Remarks*.—*Pseudoangustidontus* most strongly resembles the similarly-sized problematic genus *Angustidontus* Cooper, 1936 which ranges from the Silurian to the Carboniferous and is also known exclusively from fragmentary material. However, *Angustidontus* only exhibits a single row of spines, which are much heavier and show greater variability in length than is the case in *Pseudoangustidontus*. Although incomplete, the morphology of *Pseudoangustidontus* is sufficiently different to merit the erection of a new genus without the danger of creating synonymy.

# Discussion

A reconstruction of the fragment is given in Fig. 4. Apart from flattening, the only known specimen hardly exhibits any deformation at all, and the gross morphology of the fossil is considered to have remained largely unmodified. The specimen unequivocally shows that two rows of spines, set in a V, were present. The clear divergence between both rows of spines, becoming increasingly separated distally, precludes the interpretation of overlying spine pairs as the thickened margins of just a single spine. The slight variation in spine length observed between spines of the same type is here considered to be taphonomical; the lengths of both types of alternating spines appear to remain constant along the entire preserved length of the fragment, giving a very regular spine differentiation pattern. Similarly, the observed slight differences between the two first short spine-pairs and the other short spines may also be preservational. Because the specimen retains its greatest relief at the carinate side, this side was probably broader than the pectinate, spine-bearing side. The gradual increase in separation of the spines towards the narrow end of the fragment is considered here as an indication that, apart from the observed longitudinal curvature, the fragment also curved transversely.

Because of incomplete preservation of the only specimen, the exact nature of *Pseudoangustidontus* is unclear. One possibility is that it represents an isolated podomere. The general morphology of the fragment recalls that of the free finger of some chelicerae of certain extant pantopod and Late Palaeozoic pterygotid eurypterid chelicerates (Fig. 1F) and, among Crustacea, the chelipeds of certain decapods. A pterygotid affinity, however, can be immediately discounted: the delicate nature of the spines, and regular alternation of spine lengths in *Pseudoangustidontus* does not fit such an interpretation. Moreover, pterygotids also have single, not double spines, with the exception of the distal denticle, which is sometimes double (Kjellesvig-Waering 1964). Still, the size of *Pseudoangustidontus* is within the size range seen in pterygotid chelicerae. Among decapod crustaceans (Fig. 1H), slender, spine-bearing chelae are known from six genera belonging to the families Polychelidae, Nephropidae and Ctenochelidae, where they evolved independently at least four times and may serve for ambushing prey, and sediment raking and sieving (Tshudy and Sorhannus 2000). While some of these structures are of broadly similar dimensions as *Pseudoangustidontus*, all

← Fig. 3. Spinose appendage of the problematic arthropod *Pseudoangustidontus duplospineus* gen. et sp. nov., Arenig (Early Ordovician), Upper Fezouata Formation N of Zagora, southeastern Morocco. **A**. NMS G.2005.119.1, part. **B**. *Camera lucida*-drawing of part. **C**. NMS G.2005.119.1, counterpart. **D**. *Camera lucida*-drawing of counterpart.

these decapod chelae are evidently mineralised and only exhibit a single row of spines lacking the very regular alternation of spine lengths characteristic of *Pseudoangustidontus*. It is tempting to consider very long, slender spines to have a spearing function. Such a function for the spines of *Pseudoangustidontus*, however, seems unlikely. When the long spines would strike their prey, they effectively start functioning as levers, exacting a large force on their basal attachment points. It seems unlikely that the very long, slender spines would be able to withstand this load without breaking. This is also suggested when comparing the raptorial appendages of spearing stomatopods and mantids to *Pseudoangustidontus*: in the former two groups, fine spines are invariably much shorter, while long spines are always much sturdier than shorter ones. Another argument against a spearing function for *Pseudoangustidontus* is that it probably would be quite difficult to retrieve prey impaled on the very long spines. It therefore seems more likely that the long spines of *Pseudoangustidontus* rather functioned to immobilise prey by entangling it. Opposing spinose appendages could be brought together with their spines forming a net-like structure around the prey. In this process, the long spines may have served to limit movement of the prey, forcing it onto the intervening shorter spines. On account of their reduced length, these shorter spines would have been able to take greater loads and may indeed have had a secondary spearing function. In this scenario, it seems likely that *Pseudoangustidontus* was an ambush predator. Possibly, *Pseudoangustidontus* can be compared to the spine bearing podomeres of megalograptid or mixopterid eurypterids. Megalograptids (Fig. 1C) and mixopterids (Fig. 1D) have greatly elongated third prosomal appendages with paired spines (Caster and Kjellesvig-Waering 1964; Størmer 1934). However, the spinosity of *Pseudoangustidontus* is very different from that of these eurypterids. No eurypterid from any of these groups is known to have a podomere with more than seven pairs of spines (fifth podomere in the genus *Megalograptus* Miller, 1874), compared to the at least 39 pairs in *Pseudoangustidontus*. With the exception of the genus *Mixopterus* Ruedemann, 1921, where very short spines alternate with spines increasing in length distally, other mixopterids and megalograptids do not exhibit alternating spine lengths; all their spines rather tend to become longer distally. An alternative function for the spines of *Pseudoangustidontus* may have been to probe and sift the sediment for food. It may be comparable to the spine bearing podomeres of the sweep-feeding third and fourth prosomal appendages of Silurian laurieipterid eurypterids (Fig. 1E; Clarke and Ruedemann 1912). Laurieipterids apparently had paired spines, but like megalograptids, they have fewer spines: only around six pairs on one podomere (see *Ctenopterus cestrotus* Clarke and Ruedemann, 1912). *Laurieipterus* Kjellesvig-Waering, 1966 has spines that increase in length distally, while *Ctenopterus* was described as having spines of equal length (Clarke and Ruedemann 1912). However, it is possible that in *Ctenopterus* too, the spines actually increase in length distally (Tollerton 1989). Again, *Pseudoangustidontus* is within the size ranges seen in individual podomeres of *Megalograptus*, *Mixopterus*, and laurieipterids.

Another possible interpretation for *Pseudoangustidontus* is that it represents a large detached pectinate primary spine, carrying a double row of secondary spines on one side. If interpreted in this way, *Pseudoangustidontus* may be comparable to the pectinate spines of the Middle Cambrian anomalocaridid *Laggania cambria* Walcott, 1911 (Fig. 1B), which may have functioned to sweep the water column in search of food items (Dzik and Lendzion 1988). Further similarities may also exist to the spiculous spines of the Early Cambrian anomalocaridid *Anomalocaris briggsi* (Fig. 1A), which may have been used to probe the sediment in search of prey, with the elaborate net of secondary spines and spinules being used to encage small animals (Nedin 1995). Both types of anomalocaridid spines are of comparable size to *Pseudoangustidontus*.

Of particular importance to this discussion are the various species of the problematic genus *Angustidontus* Cooper, 1936, described from the Silurian to the Carboniferous. Like *Pseudoangustidontus*, all specimens of *Angustidontus* consist of isolated elongated fragments carrying a high number of spines of varying lengths (Fig. 1G). They have variously been allied to vertebrates (Cooper 1936), eurypterids (Briggs 1979; Raasch 1956; Ruedemann 1935), and stomatopod crustaceans (Copeland and Bolton 1960). A vertebrate identity, however, seems unlikely given the lack of identifiable bone histology and apatite (David H. Dunkle, personal communication to Walter Youngquist 1955). Kjellesvig-Waering (1964) rejected a eurypterid affinity for angustidontids, a view shared by Victor P. Tollerton Jr (personal communication 2005) and also supported here. Nevertheless, Briggs (1979) and Braddy and Dunlop (2000) still refused to rule out a eurypterid affinity for angustidontids. A stomatopod affinity is also unlikely: the varying spine-lengths characteristic of *Angustidontus* are unknown from any stomatopod (Braddy and Dunlop 2000). Another possibility is that angustidontids are part of some kind of chelate arthropod appendage (Rodney M. Feldmann, personal communication 2005). A problem with this interpretation is that so far no other chelate appendage fragments attributable to this group have been found. Nevertheless, *Angustidontus* indeed shows a resemblance to the fingers of the chelae of some decapod crustaceans mentioned above. Although this similarity most likely results from convergence, a crustacean affinity for angustidontids still seems plausible. One more possibility that cannot be discounted is that specimens of *Angustidontus*, as suggested here for *Pseudoangustidontus*, in fact represent some kind of detached pectinate spines. The alternating spine length, and the high number of spines and a similar size are characters *Pseudoangustidontus* shares with *Angustidontus*. However, none of the species belonging to the latter genus exhibits a carina. They also have a lower number of spines than

*Pseudoangustidontus*, and angustidontid spines are invariably much heavier. Another, more important characteristic setting *Pseudoangustidontus* apart from *Angustidontus* is the possession of a double row of spines: all known angustidontids only possess a single row of spines. Moreover, the alternation of spine lengths in angustidontids is not as regular as seen in the Moroccan fossil: the irregular occurrence of up to five different spine lengths in angustidontids necessitates the use of a special formula for distinguishing between the various spine-sizes (Copeland and Bolton 1960).

# Conclusions

At present, it seems a megalograptid eurypterid affinity for the new fossil still cannot be ruled out entirely, in which case *Pseudoangustidontus* would be the oldest eurypterid known. However, the Moroccan fossil is rather different from anything currently known from the Eurypterida. Of all arthropods discussed above, *Pseudoangustidontus* appears most similar to the angustidontids, and if considered to belong to this group, it would be its oldest representative by far. However, differences in spine organisation still appear to differentiate these groups. The problem is that both groups are known only from very fragmentary material, making it difficult to judge their exact morphology and the importance of the differences separating *Pseudoangustidontus* and *Angustidontus*. The differences of *Pseudoangustidontus* to both megalograptids and angustidontids may, in fact, be a result of the great antiquity of the former when compared to representatives of the latter groups. Although the unmineralised fossil clearly does not belong to any of the previously discussed calcitic decapod crustacean taxa, a general crustacean affinity for *Pseudoangustidontus* still cannot be ruled out completely. However, because none of the groups discussed above comes close to matching the morphology described for *Pseudoangustidontus*, it is plausible that any similarities that do exist are superficial and the result of convergence. Therefore, the possibility that the specimen belongs to an as yet undiscovered arthropod group remains open.

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